Ecological study on the relationship between plant biodiversity and soil fertility in a mature tropical forest, Costa Rica

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Key words: Shannon-Wiener diversity, Simpson's diversity, Soil chemical fertility, Species richness, Structural diversity, Structural richness, Tropical forest

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Abstract

The relationship between plant biodiversity and soil chemical fertility has been widely investigated in temperate forests and agroecosystems, but there is lack of information about the correlation between these two variables in tropical forests. In this study, the relationship between plant biodiversity and soil chemical fertility was analyzed in a mature tropical forest in Costa Rica. Soil samples were collected in 9 sampling plots (5 m by 25 m) in order to identify the concentration level of P, K, Ca, Mg, Fe, Zn, Mn, and Cu, the soil fertility index, the CEC, and the C/N ratio. Furthermore, species richness, Shannon-Wiener and Simpson's species diversity, structural richness, and structural diversity were determined for each of the 9 sampling plots. Simple linear regression analysis was used to determine if there was a significant relationship between any of the different variables of plant biodiversity and soil chemical fertility. Tree species richness was inversely related to concentration levels of K, Ca, and P, CEC, and soil fertility index. These results agree with the few studies that were done in tropical ecosystems. Higher tree species richness tended to be found in sites with lower soil fertility. Shannon-Wiener tree species diversity was positively correlated to C/N ratio. This is a new discovery and it seems that there is less N stored in organic matter compared to C in sites with higher

species diversity. Herb structural richness was positively related to soil fertility index and P concentration. The herb community may be able to grow taller in soil with higher P content and soil fertility leading to higher structural richness because P is the main soil factor limiting growth in tropical ecosystems. There was a positive relationship between herb structural diversity and Mn concentration in the soil. Therefore, structural diversity is not affected much by soil fertility. No relationship was found among any of the other variables. This study gives important insights on the ecological relationship between plant biodiversity and soil chemical fertility in primary tropical forest stands.

Introduction

Tropical forest ecosystems are known for having the highest plant biodiversity on the planet. Amazonian tropical forest can support life for more than 280 tree species per hectare (Wright 2002). In Ecuador, 1104 tree species were found living in an area of 25 ha (Wright 2002). This high plant biodiversity is essential for the survival of several living organisms that thrive in tropical ecosystems. It is thought that high plant biodiversity of the tropics is mainly caused by factors such as high stable temperature (low seasonality), high humidity (high precipitation), and high solar radiation all year round which favour the growth of a large number of species (Givnish 1999). Although the main causal factors of plant biodiversity are related to climate and topography, it is important to understand what is happening at the microhabitat level. Does soil fertility have any effects on plant biodiversity in a mature tropical forest? Conversely, does plant biodiversity have any effects on soil fertility in tropical ecosystems? Is there a relationship between the two?

Literature review

Waide *et al.* (1999) have reviewed literature on the relationship between plant productivity and species richness in desert, boreal forest, tropical forest, and wetland ecosystems. They concluded that the data available are not enough to resolve the extent of the relationship because the patterns are so variable. In 200 relationships reviewed, 26% were positive and linear, 12% were negative and linear, 30% were unimodal, and 32% were not significant. On this discovery, Waide *et al.* (1999) suggested that the relationship may vary according to different habitats, and also to other factors related to plant productivity and species richness.

Furthermore, Partel *et al.* (2007) investigated plant diversity-productivity relationship patterns from 163 case studies all around the world. They found that around 80% of the relationship variation was explained by latitude. The unimodal relationship in which productivity is low at low and very high diversity and is high at medium diversity seems to dominate the temperate regions. On the other hand, the positive relationship in which productivity increases concurrently with plant diversity seemed to be significantly more common in the tropical regions.

On more specific research, Janssens *et al.* (1998) have looked at the relationship between plant biodiversity and different soil chemical factors in numerous sites located in grassland ecosystems of temperate regions. They found a positive relationship between plant biodiversity and the concentration of extractable phosphorus and potassium in the soil. Potassium was related to species richness. Higher species richness gave potassium concentrations closer to the optimum level for plant nutrition. Also, potassium content in the soil was higher with higher values of species diversity. Conversely, phosphorus was only related to species richness. There was no relationship found between plant biodiversity and other factors such as nitrogen content, calcium content, pH, and organic matter.

Tilman *et al.* (1996) used a well-replicated experiment of 147 plots in temperate regions, in which species richness and Shannon-Wiener species diversity were directly controlled through different treatments of plant biodiversity, to investigate the effects of species richness and diversity on ecosystem productivity. They found that more nitrogen, which is the main limiting factor in these regions, was available to plant roots in plots with higher species richness and diversity due to the reduction of nitrogen leaching loss in the soil; thereby increasing ecosystem productivity at the same time.

In a different approach, Holl (1999) measured vegetation, microclimate, soil physical and chemical parameters, seed rain, and seed germination in an abandoned pasture and a near primary tropical forest of southern Costa Rica. He found that the levels of most soil nutrients, especially phosphorus, were usually lower in the pasture compared to the forest containing higher plant biodiversity. This study further showed that phosphorus is an important soil limiting factor in tropical ecosystems. Nitrogen, calcium, and magnesium had medium to high concentration levels in pasture soil, but they were still a little bit lower than in primary tropical forest.

In more recent research, Dybzinski *et al.* (2008) studied the effects of plant species diversity on productivity in a grassland ecosystem of Minnesota in the United States. They grew seedlings of *Echinacea purpurea* (purple coneflower) in soil that was collected from 10-year-old experimental plots consisting of 1,2,4,8, or 16 native grassland species. Plant biomass and concentration of N, P, K, Ca, and Mg were measured. They found that the soil from the higher plant species diversity plots was producing more biomass than the soil from lower plant diversity plots and this phenomenon was caused by greater soil nitrogen availability, which is the limiting factor for these ecosystems. Also, they discovered that the increase of biomass with diversity enhanced nitrogen inputs and retention. Therefore, Dybzinski *et al.* (2008) suggested that higher plant species diversity may increase community productivity through the increase of nutrient supply via greater inputs and retention.

Furthermore, Kumar *et al.* (2010) studied the relationship between tree species diversity and soil nutrient concentration in three different sites of dry deciduous forest of western India. They measured tree stand density, Shannon-Wiener and Simpson's species diversity, and species richness, and they collected soil samples in each of three sites. The phosphorus, nitrogen, and carbon content of each sample were analyzed. They found that there was a strong positive correlation between the content of N, P, and C and tree species richness. Furthermore, tree density was negatively correlated with phosphorus and nitrogen content and positively correlated with carbon content.

Study objectives and important concept definitions

Much research on the relationship of plant biodiversity with productivity and soil fertility has been done in grassland ecosystems, temperate forest stands, and agroecosystems. On the other hand, there is a lack of research and data available about the correlation between plant biodiversity and soil fertility in tropical forest ecosystems. In this study, I will be investigating if there is a relationship between plant biodiversity and soil chemical fertility in a mature tropical forest in Costa Rica. Therefore, I will determine plant biodiversity and soil chemical fertility in different sampling plots randomly chosen in the study area. This study will increase our knowledge and help understand better the relationship between these two variables. The hypothesis is that there should be relationships between plant biodiversity measurements (species richness, Shannon-Wiener and Simpson's species diversity, structural richness and diversity) and soil chemical fertility factors (concentration of K, Ca, Mg, P, Fe, Cu, Zn, and Mn, CEC, C/N ratio, soil fertility index, Total N and C in organic matter).

Before going further in this research, some important concepts need to be clarified. Plant species biodiversity can be measured using different approaches including species richness, Shannon-Wiener species diversity, Simpson's species diversity, structural richness, and structural diversity (Whittaker 1972). Species richness is the number of species of plants in a given area. Shannon-Wiener species diversity is a measure of evenness and is affected by both the number of species and evenness of the community (Whittaker 1972). Higher evenness in the abundance of species leads to higher diversity in a community (Whittaker 1972). Simpson's species diversity measures the probability that two individuals randomly selected from a sample will belong to different species and is directly affected by the abundance of species in a community (Whittaker 1972). Higher values mean higher diversity. Structural richness is the number of plant height classes in a stand (Bohl and Lanz 2002). On the other hand, structural diversity (S-W) refers to the number of layers (microhabitats) in a stand (Bohl and Lanz 2002). Diversity is higher when species richness, structural richness and structural diversity are high. In this study, all of these approaches will be used to measure plant biodiversity. In addition, another important concept needs to be defined: soil chemical fertility. In this study, soil chemical fertility involves the availability (concentration) of the following elements of the soil (nutrients: N, P, K, Ca, Mg, Fe, Zn, Mn) for plant uptake, the cation exchange capacity (CEC), and the C/N ratio in organic matter.

Study Area

The data for this study were collected in the ‘’Reserva Biológica Alberto Manuel Brenes’’, district of San Ramón, in the province of Alajuela, Costa Rica (Figure 1). It is located in the beginning of the mountain chain of ‘’Cordillera de Tilarán’’ on the Pacific side (Figure 1). It is a biological reserve of 7800 ha consisting of mature tropical forests with elevation varying between 800 m and 1500 m above sea level. The precipitation varies between 3500 mm and 6000 mm per year and the temperature ranges from 17℃ to 25℃ with an annual average of 21℃. This kind of climate and variable topography results in the presence of three types of forest called Pre-mountain humid forest, Pre-mountain very humid forest, and Lower mountain humid forest. The forest types were identified using the system of life zones created by Holdridge (Holdridge 1947).

Figure 1: Map of the location of the study area ''Reserva Biológica Alberto Manuel Brenes de San Ramón'' en Costa Rica.

The reserve is located in an area known for its soil classified as Inceptisols and Ultisoles which tend to be moderately acid and contain low concentration levels of calcium, magnesium, potassium, and zinc. The relief tends to be abrupt and it shelters high plant species richness in which 1012 species of angiosperms were identified (Salazar-Rodríguez 2000).

Methods

Inventory of plant family composition and abundance, and Biodiversity calculation

Data were collected during 5 days in early December 2011. Three sampling plots of 5 m by 25 m area were selected randomly in each of the three life zones (Pre-mountain humid forest, Pre-mountain very humid forest, and Lower mountain humid forest) located in the ''Reserva Biológica Alberto Manuel Brenes'' (Stickney 1980). Therefore, there were 9 sampling plots analysed in this study. Each plot was divided into five units of 5 m by 5 m and the abundance and height class of the different tree species were measured in each of these units (Stickney 1980). Also, the abundance and height class of the different shrub species were measured from a 3 m by 3 m area within each 5 m by 5 m unit(Stickney 1980). Furthermore, the abundance and height class of the different herb species were measured from a 1 m by 1 m area within each 3 m by 3 m sampling unit (Stickney 1980). The figure below shows how the sampling plots were laid out (Figure 2). The abundance and height class of each plant species were recorded into a table in the field. Bamboo sticks were used to delimit the area of the sampling plots. The identification of the plant species was done using the knowledge of Costa Rica flora gained by the people in the field and plant identification guides. When it was not possible to identify the species in the field, a sample was collected and brought to Carlos Morales, a specialist in Botany at the University of Costa Rica. Epiphytes, vines, and lianas were not included in this study. Tree pruning tools were used to cut a small branch of trees in order to identify their species.

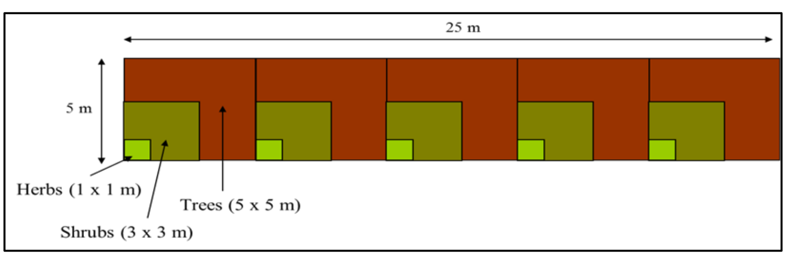

Figure 2: Vegetation sampling plot for measuring abundance and height class of herbs, shrubs, and trees.

In each sampling plot, the abundance was measured by estimating the percentage of ground that was covered by a plant species if we were looking at it from above the canopy. The area covered (m^2) by a plant species per hectare was calculated by multiplying the percentage of ground cover, the area of the plot, and the number of plots that fits in one hectare. The height class was measured using a stick which indicates 6 different height classes (0-10 cm, 11-30 cm, 0.3-1 m, 1-3 m, and 3-10 m, ≥ 10 m). Once the area covered and the height class of the plant species had been measured, the crown volume index was calculated by multiplying the area covered by the height. The mean crown volume index was calculated by averaging the crown volume index of the 5 sub-plots in a sampling plot. This mean crown volume index represents the space occupied by each plant species in a sampling plot per 0.01 ha.

Total crown volume index (m^3/0.01 ha) of all species together (herbs, shrubs, and trees separately) was calculated for each sampling plot by adding the mean crown volume index of plant species together. Plant biodiversity was determined by calculating species richness, Shannon-Wiener species diversity, Simpson's species diversity, structural richness, and structural diversity (S-W). Species richness was calculated by counting the number of species that was recorded in each sampling plot. Shannon-Wiener species diversity was calculated by first calculating the proportion that each plant species had in the community (crown volume index of a species / total volume of all species), then multiplying the proportion of each species by $\log_2$, and finally adding the results from the previous calculation together and multiplying it by "-1". Simpson's species diversity was calculated by subtracting the sum of the square of proportion from "1". Structural richness was calculated by counting the number of height classes recorded for each unit and averaging it for each sampling plot. Structural diversity (S-W) was calculated by first calculating the proportion that each height class had in the community (crown volume index of plants located in a height class / total volume of plants in all height classes), then multiplying the proportion of each height class by $\log_2$, and finally adding the results from the previous calculation together and multiplying it by "-1".

Collection of soil samples and analysis

In each sampling plot, three samples of soil and organic matter were collected in order to identify the concentration level of macronutrients (P, K, Ca, Mg) and micronutrients (Fe, Zn, Mn, Cu), the cation exchange capacity in the soil, and the C/N ratio in the organic matter (Figure 3). Each soil sample collected was around 1000 cm^3 of volume and was taken from horizon A. Each organic matter sample was also around 1000 cm^3 of volume and was taken from the forest floor. Soil and organic matter samples were put in plastic bags marked with a sample number and they were brought to the lab for analysis after the 5-day trip to the field. These soil and organic matter samples were analysed in the soil lab of ‘’Cafesa’’ in San José, Costa Rica. Olsen modified method was used to determine the concentration levels of K, P, Fe, Cu, Zn, and Mn (Olsen *et al.* 1954). KCl 1N method was used to determine the concentration levels of Ca, Mg, and extractable acids (Lin and Coleman 1960). Soil fertility index for tropical ecosystems was calculated by adding the percentage values of the concentration of P, K, and Ca obtained by dividing the concentration of each sampling plot by the mean concentration of the 9 sampling plots (Huston 1980).

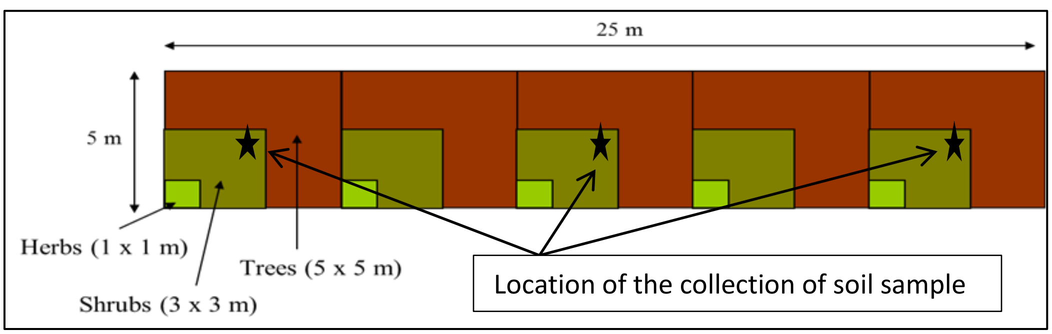

Figure 3: Location of where the soil sample will be collected in each sampling plot.

Statistical analysis

Simple linear regression analysis was used to identify if there was a positive or negative relationship between the different plant biodiversity measurements (species richness, Shannon-Wiener diversity, Simpson’s diversity, structural richness, and structural diversity) and the different soil fertility variables (K, Ca, Mg, P, Fe, Cu, Zn, Mn, CEC, C/N ratio, total N, organic C, and soil fertility index). Analysis of variance for regression was used to calculate *P*-values and to see if the regressions were significant (Kozak *et al.* 2008). The correlation coefficient was calculated using the equation ''$r = \sqrt{(SS_{Reg}/SS_T)}$'' and the analysis of variance for regression (Kozak *et al.* 2008). In all analyses, the level of significance was $P = 0.05$.

Results

Relationships between Potassium (K) and the different plant biodiversity measurements

Linear regression analysis indicated that tree species richness was negatively related to concentration level of K in the soil (Figure 4). This relationship was found to be significant ($P = 0.04$ and r = 0.69) (Table 1). The regression equation that describes this relationship was: Tree species richness = -38.91 (concentration level of K) + 38.9 (Figure 4). We can see that the number of tree species declines as the concentration level of K increases. On the other hand, there was no relationship between the concentration level of K and species richness for either the herb community ($P = 0.91$, r = 0.04) or the shrub community ($P = 0.63$, r = 0.19).

Table 1: Analysis of variance for regression (Relationship between potassium concentration and tree species richness)

	Degree of freedom	*Sum of square*	*Mean Square*	*F*	*P-value*
Regression	1	214.41	214.41	6.42	0.04
Residual error	7	233.81	33.40		
Total	8	448.22			

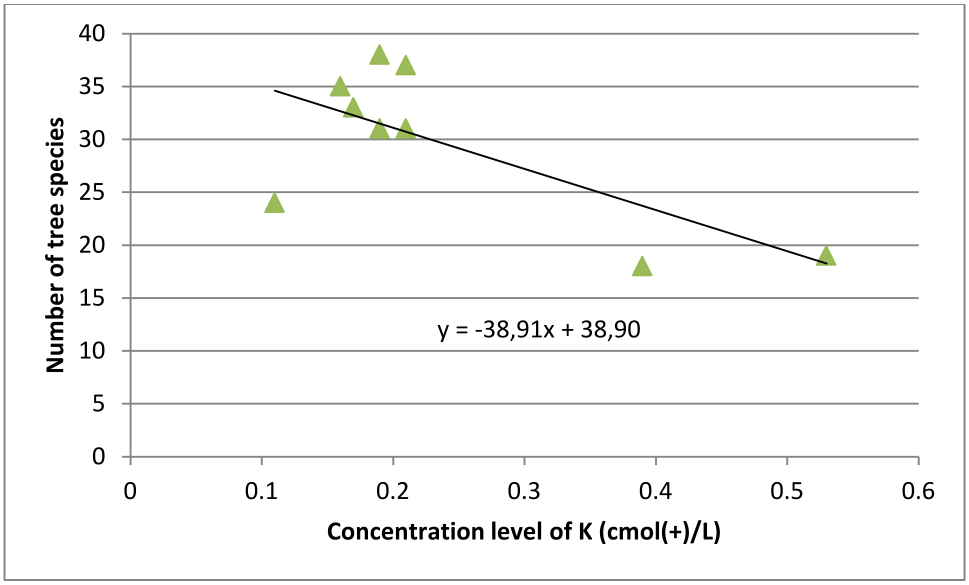

Figure 4: Tree species richness as a function of the concentration level of Potassium (K) in cmol(+)/L.

No relationship was discovered between concentration of K in the soil and Shannon-Wiener species diversity of herbs (*P* = 0.20, r = 0.47), shrubs (*P* = 0.47, r = 0.28), and trees (*P* = 0.31, r = 0.38). Furthermore, there was no relationship encountered between concentration level of K and Simpson's species diversity of herbs (*P* = 0.11, r = 0.57), shrubs (*P* = 0.74, r = 0.13), and trees (*P* = 0.81, r = 0.09).

There was no relationship between herb structural richness and concentration level of K (*P* = 0.08, r = 0.61) (Figure 5; Table 2). However, it was close to be significant with a positive relationship. No relationship was observed between K concentration and structural richness of shrubs (*P* = 0.33, r = 0.37) and trees (*P* = 0.61, r = 0.20). Also, structural diversity of herbs (*P* = 0.27, r = 0.41), shrubs (*P* = 0.22, r = 0.46), and trees (*P* = 0.61, 0.20) was not correlated to K concentration.

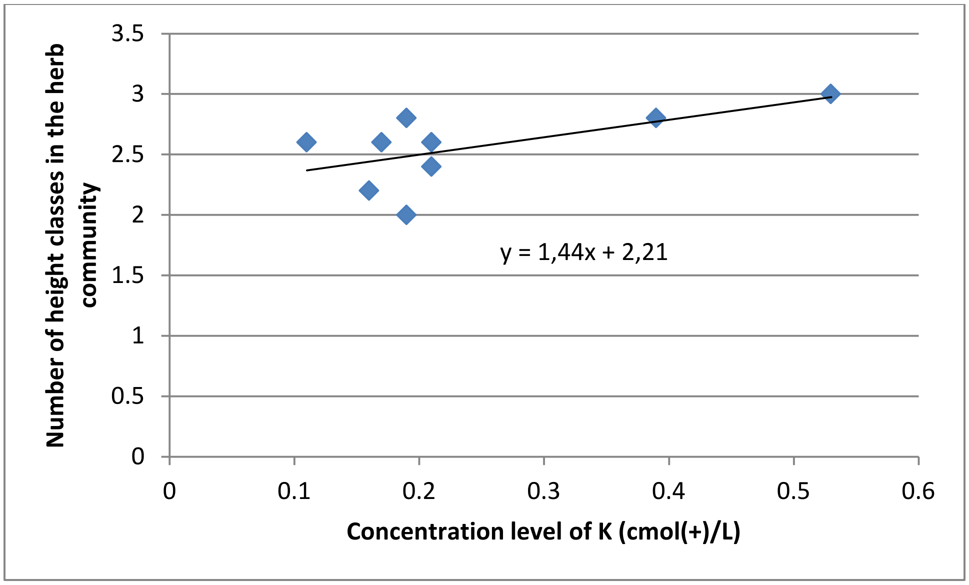

Figure 5: Herb structural richness as a function of the concentration of Potassium (K) in cmol(+)/L.

Table 2: Analysis of variance for regression (Relationship between potassium concentration and herb structural richness)

	Degree of freedom	*Sum of squares*	*Mean squares*	*F*	*P-value*
Regression	1	0.29	0.29	4.21	0.08
Residual error	7	0.49	0.07		
Total	8	0.78			

Relationships between Calcium (Ca) and the different plant biodiversity measurements

Tree species richness was inversely related to Ca concentration in the soil (Figure 6). This relationship was found to be significant (*P* = 0.05, r = 0.67) (Table 3). We can see that tree species richness decreased as the concentration level of Ca increased in this mature tropical forest (Figure 6). The regression equation was: Tree species richness = -2.82 (Ca concentration) + 39.24. Conversely, there was no relationship encountered between Ca concentration and species richness of herbs (*P* = 0.93, r = 0.04) and shrubs (*P* = 0.40, r = 0.32).

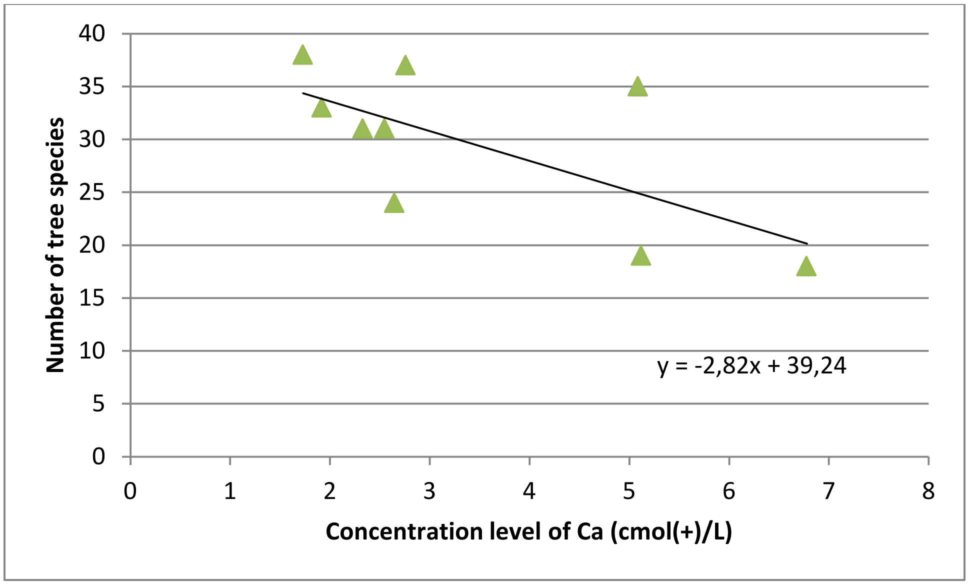

Figure 6: Tree species richness as a function of the concentration level of Calcium (Ca) in cmol(+)/L.

Table 3: Analysis of variance for regression (Relationship between calcium concentration and tree species richness)

	Degree of freedom	*Sum of squares*	*Mean squares*	*F*	*P-value*
Regression	1	198.92	198.92	5.59	0.05
Residual error	7	249.30	35.61		
Total	8	448.22			

Ca concentration was not correlated to Shannon-Wiener species diversity of herbs (P = 0.17, r = 0.50), shrubs (P = 0.57, r = 0.22), and trees (P = 0.98, r = 0.01), neither to Simpson's species diversity of herbs (P = 0.26, r = 0.42), shrubs (P = 0.74, r = 0.13), and trees (P = 0.57, r = 0.22). Additionally, Ca concentration was not related to structural richness of herbs (P = 0.33, r =0.37), shrubs (P = 0.86, r = 0.07), and trees (P = 0.99, r = 0.006), neither to structural diversity of herbs (P = 0.46, r = 0.28), shrubs (P = 0.94, r = 0.03), and trees (P = 0.21, r = 0.46).

Relationships between Magnesium (Mg) and the different plant biodiversity measurements

Mg concentration in the soil was close to being negatively correlated to tree species richness (*P* = 0.05, correlation coefficient (r) = 0.66) (Figure 7; Table 4). Furthermore, the data demonstrated that there was no relationship between magnesium concentration and species richness of herbs (*P* = 0.82, r = 0.09), shrubs (*P* = 0.33, r = 0.37).

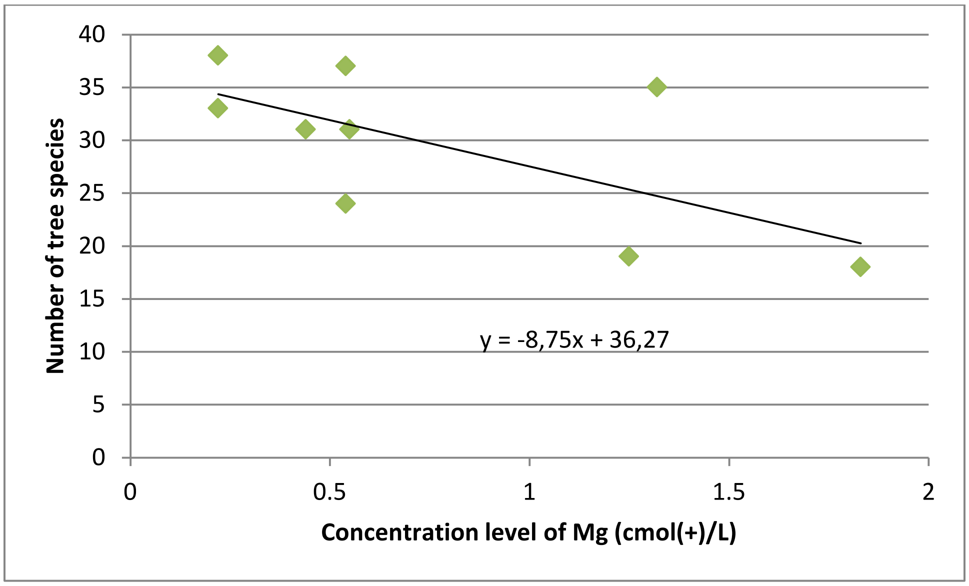

Figure 7: Trees species richness as a function of the concentration of Magnesium (Mg) in cmol(+)/L.

Table 4: Analysis of variance for regression (Relationship between magnesium concentration and tree species richness)

	Degree of freedom	*Sum of squares*	*Mean squares*	*F*	*P-value*
Regression	1	193.27	193.27	5.31	0.054
Residual error	7	254.95	36.42		
Total	8	448.22			

Mg concentration was not related to Shannon-Wiener species diversity of herbs (*P* = 0.18, r = 0.49), shrubs (*P* = 0.55, r = 0.23), and trees (*P* = 0.98, r = 0.01), neither to Simpson's species diversity of herbs (*P* = 0.27, r = 0.41), shrubs (*P* = 0.73, r = 0.13), trees (*P* = 0.59, r = 0.21). Also, Mg concentration was not correlated to structural richness of herbs (*P* = 0.35, r = 0.35), shrubs (*P* = 0.92, r = 0.04), and trees (*P* = 0.98, r = 0.01), neither to structural diversity of herbs (*P* = 0.43, r = 0.30), shrubs (*P* = 0.98, r = 0.01), trees (*P* = 0.25, r = 0.43).

Relationships between Phosphorus (P) and the different plant biodiversity measurements

P concentration in the soil was inversely correlated to tree species richness (Figure 8). The regression was significant (*P* = 0.047, r = 0.67) (Table 5). Therefore, tree species richness decreased as P concentration increased (Figure 8). The regression equation was: Tree species richness = -1.55 (phosphorus concentration) + 38.67. On the other hand, there was no relationship between P concentration and species richness of herbs (*P* = 0.86, r = 0.07) and shrubs (*P* = 0.97, r = 0.01).

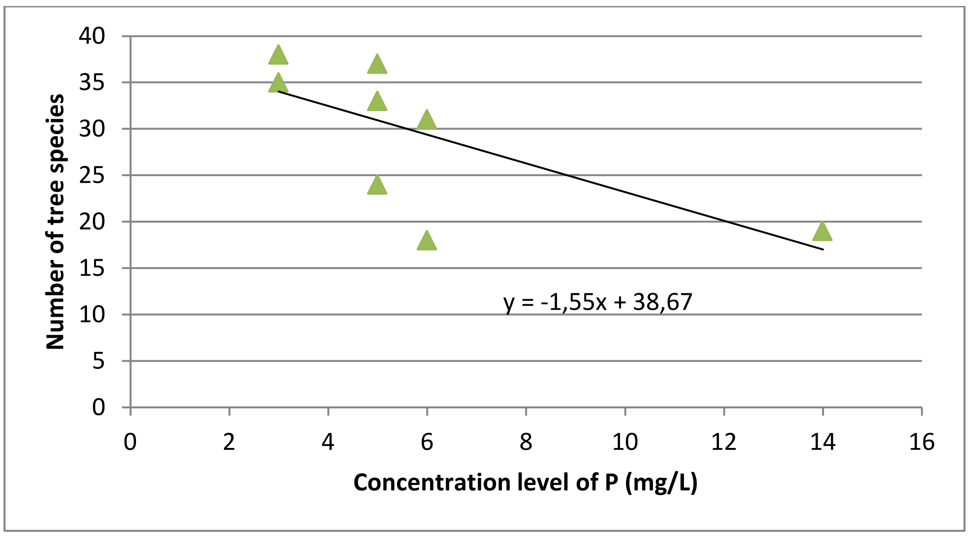

Figure 8: Tree species richness as a function of the concentration level of Phosphorus (P) in in mg/L.

Table 5: Analysis of variance for regression (Relationship between phosphorus concentration and tree species richness)

	Degree of freedom	*Sum of squares*	*Mean squares*	*F*	*P-value*
Regression	1	203.53	203.53	5.82	0.047
Residual error	7	244.69	34.96		
Total	8	448.22			

P concentration was not related to Shannon-Wiener species diversity of herbs (*P* = 0.31, r = 0.38), shrubs (*P* = 0.24, r = 0.44), and trees (*P* = 0.17, r = 0.50). As well, it was not related to Simpson's species diversity of herbs (*P* = 0.24, r = 0.43), shrubs (*P* = 0.42, r = 0.31), and trees (*P* = 0.59, r = 0.21).

Herb structural richness was positively correlated to P concentration (Figure 9). The regression was significant (*P* = 0.01, r = 0.78) (Table 6). Therefore, herb structural richness increased as P concentration augmented (Figure 9). The regression equation was: Herb structural richness = 0.07 (P concentration) + 2.11 (Figure 9). There was no relationship between P concentration and structural richness of shrubs (*P* = 0.16, r = 0.51) and trees (*P* = 0.27, r = 0.41).

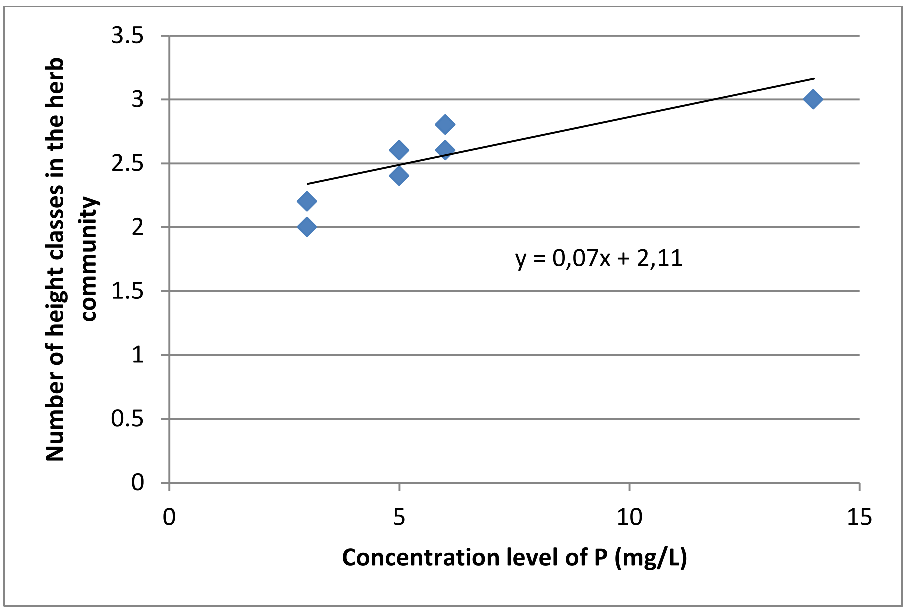

Figure 9: Herb structural richness as a function of the concentration level of Phosphorus (P) in mg/L.

Table 6: Analysis of variance for regression (Relationship between phosphorus concentration and herb structural richness)

	Degree of freedom	*Sum of squares*	*Mean squares*	*F*	*P-Value*
Regression	1	0.48	0.48	10.87	0.01
Residual error	7	0.31	0.04		
Total	8	0.78			

P concentration was almost positively related to herb structural diversity with *P* = 0.09 and r = 0.59 (Figure 10; Table 7). There was no relationship between P concentration and structural diversity of shrubs (*P* = 0.15, 0.52) and trees (*P* = 0.67, r = 0.16).

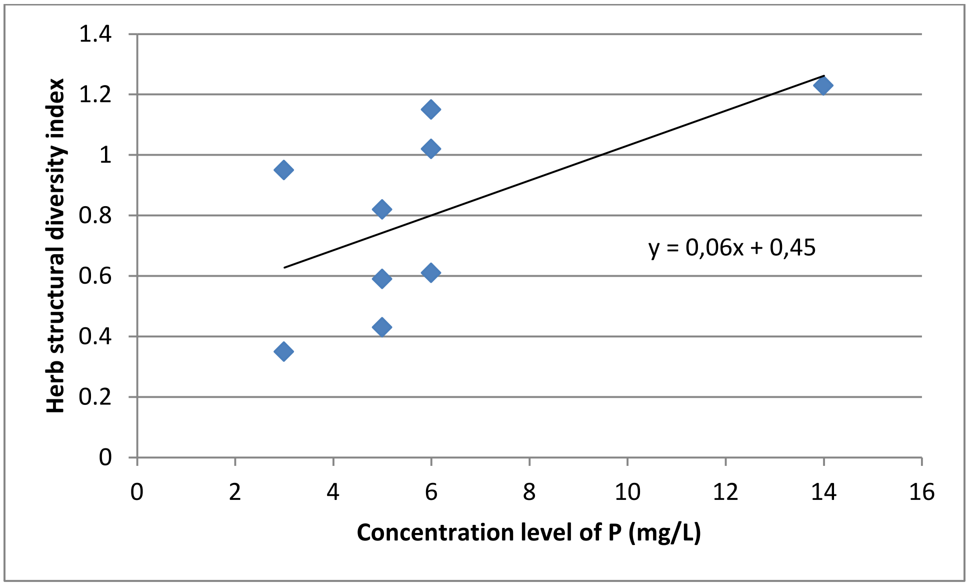

Figure 10: Herb structural diversity as a function of the concentration level of Phosphorus (P) in mg/L.

Table 7: Analysis of variance for regression (Relationship between phosphorus concentration and herb structural diversity)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.28	0.28	3.83	0.09
Residual error	7	0.52	0.07		
Total	8	0.80			

Relationships between Iron (Fe) and the different plant biodiversity measurements

There was no relationship between Fe concentration in the soil and species richness of herbs (*P* = 0.59, r = 0.21), shrubs (*P* = 0.83, r = 0.08), and trees (*P* = 0.29, r = 0.40). Additionally, Fe concentration was not related to Shannon-Wiener species diversity of herbs (*P* = 0.64, r = 0.18), shrubs (*P* = 0.67, r =

0.17), and trees (*P* = 0.46, r = 0.28), neither to Simpson's species diversity of herbs (*P* = 0.31, r = 0.38), shrubs (*P* = 0.89, r = 0.05), and trees (*P* = 0.82, r = 0.09).

Tree structural richness was almost positively correlated to Fe concentration, but the regression was not significant (*P* = 0.06, r = 0.65) (Figure 11; Table 8). There was no relationship between Fe concentration and structural richness of herbs (*P* = 0.16, r = 0.51) and shrubs (*P* = 0.41, r = 0.31).

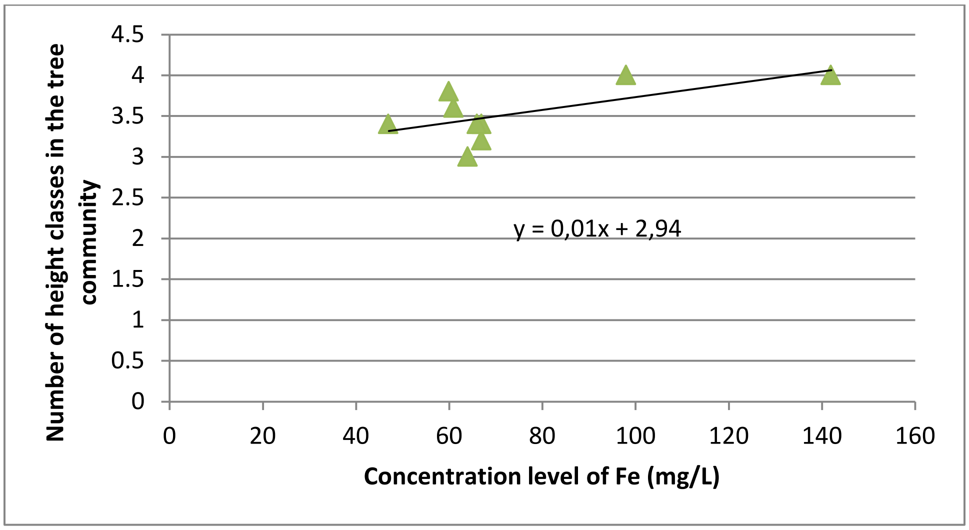

Figure 11: Tree structural richness as a function of the concentration level of Iron (Fe) in mg/L.

Table 8: Analysis of variance for regression (Relationship between iron concentration and tree structural richness)					
	Degree of freedom	*Sum of squares*	*Mean squares*	*F*	*P-value*
Regression	1	0.41	0.41	5.14	0.06
Residual error	7	0.55	0.08		
Total	8	0.96			

Herb structural diversity was almost positively related to Fe concentration, but the regression was not significant (*P* = 0.06, r = 0.65) (Figure 12; Table 9). On the other hand, there was no relationship between Fe concentration and structural diversity of shrubs (*P* = 0.33, r = 0.37) and trees (*P* = 0.91, r = 0.04).

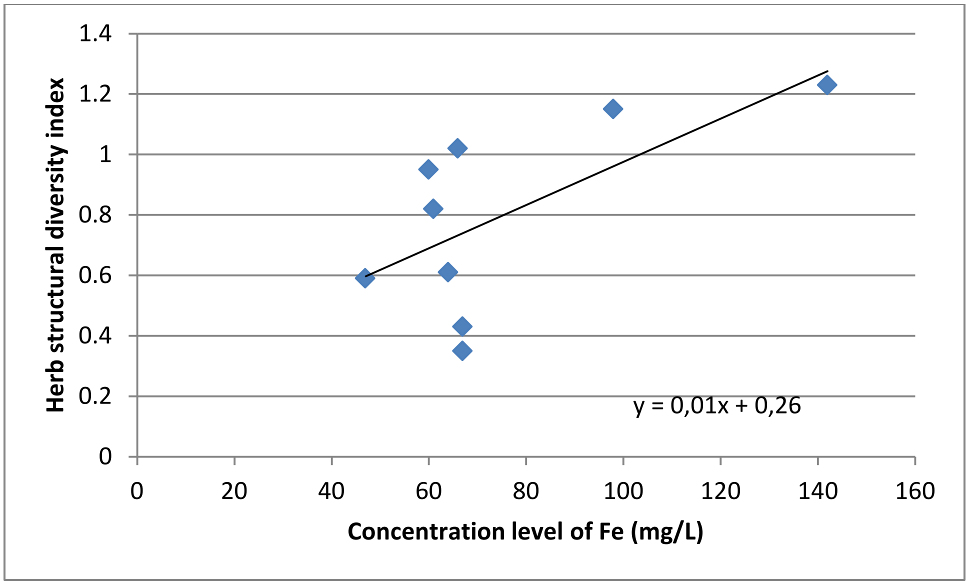

Figure 12: Herb structural diversity as a function of the concentration level of Iron (Fe) in mg/L.

Table 9: Analysis of variance for regression (Relationship between iron concentration and herb structural diversity)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.34	0.34	5.07	0.06
Residual error	7	0.46	0.07		
Total	8	0.80			

Relationships between Copper (Cu) and the different plant biodiversity measurements

There was no relationship between Cu concentration in the soil and species richness of herbs (*P* = 0.35, r = 0.35), shrubs (*P* = 0.74, r = 0.13), and trees (*P* = 0.43, r = 0.30). Also, Cu concentration was not correlated to Shannon-Wiener species diversity of herbs (*P* = 0.57, r = 0.22), shrubs (*P* = 0.32, r = 0.38), and trees (*P* = 0.52, r = 0.25), neither to Simpson's species diversity of herbs (*P* = 0.14, r = 0.53), shrubs (*P* = 0.37, r = 0.34), and trees (*P* = 0.76, r =0.12). Even more, Cu concentration was not related to structural richness of herbs (*P* = 0.85, r = 0.08), shrubs (*P* = 0.43, r = 0.30), and trees (*P* = 0.42, r = 0.31), neither to structural diversity of herbs (*P* = 0.35, r =0.35), shrubs (*P* = 0.57, r = 0.22), and trees (*P* = 0.88, r = 0.06).

Relationships between Zinc (Zn) and the different plant biodiversity measurements

There was no relationship between Zn concentration in the soil and species richness of herbs (*P* = 0.36, r =0.35), shrubs (*P* = 0.32, r = 0.38), and trees (*P* = 0.96, r = 0.02). Furthermore, Zn concentration was not related to Shannon-Wiener species diversity of herbs (*P* = 0.81, r = 0.09), shrubs (*P* = 0.48, r = 0.27), and trees (*P* = 0.91, r = 0.04), neither to Simpson's species diversity of herbs (*P* = 0.79, r = 0.10), shrubs (*P* = 0.70, r = 0.15), and trees (*P* = 0.78, r = 0.11). There was no relationship between Zn concentration and structural richness of herbs (*P* = 0.45, r = 0.29), shrubs (*P* = 0.50, r = 0.26), and trees (*P* = 0.14, r = 0.53). Zn concentration was almost correlated to shrub structural diversity, but the regression was not significant (*P* = 0.08, r = 0.61) (Figure 13; Table 10). Also, there was no relationship between Zn concentration and structural diversity of herbs (*P* = 0.104, r = 0.58) and trees (*P* = 0.63, r = 0.19)

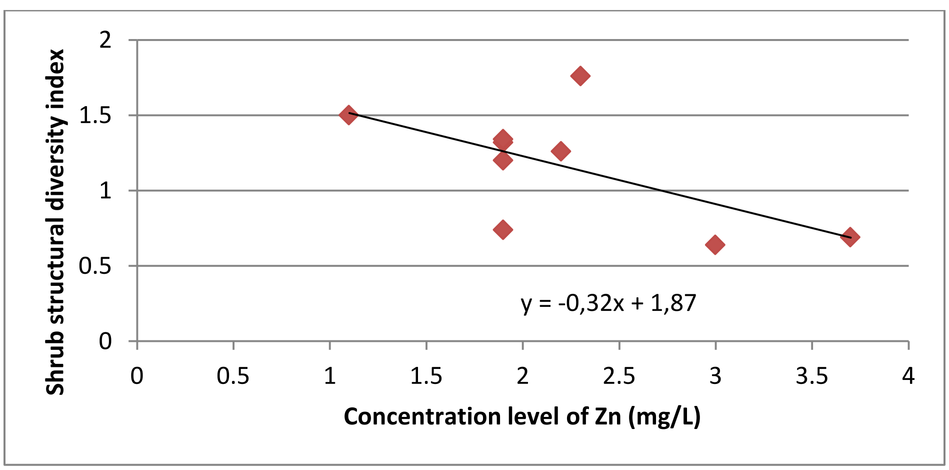

Figure 13: Shrub structural diversity as a function of the concentration level of Zinc (Zn) in mg/L.

Table 10: Analysis of variance for regression (Relationship between zinc concentration and shrub structural diversity)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.45	0.45	4.18	0.08
Residual error	7	0.76	0.11		
Total	8	1.21			

Relationships between Manganese (Mn) and the different plant biodiversity measurements

There was no relationship between Mn concentration in the soil and species richness of herbs (*P* = 0.94, r = 0.03), shrubs (*P* = 0.62, r = 0.19), and trees (*P* = 0.11, r = 0.57). Furthermore, Mn concentration was not related to Shannon-Wiener species diversity of herbs (*P* = 0.20, r = 0.47), shrubs (*P* = 0.26, r = 0.42), and trees (*P* = 0.33, r = 0.37), neither to Simpson's species diversity of herbs (*P* = 0.32, r = 0.38), shrubs (*P* = 0.48, r = 0.27), and trees (*P* = 0.72, r = 0.14).

Mn concentration was almost positively correlated to herb structural richness, but the regression was not significant (*P* = 0.067, r = 0.63) (Figure 14; Table 11). Also, there was no relationship between Mn concentration and structural richness of shrubs (*P* = 0.52, r = 0.25) and trees (*P* = 0.15, r = 0.52).

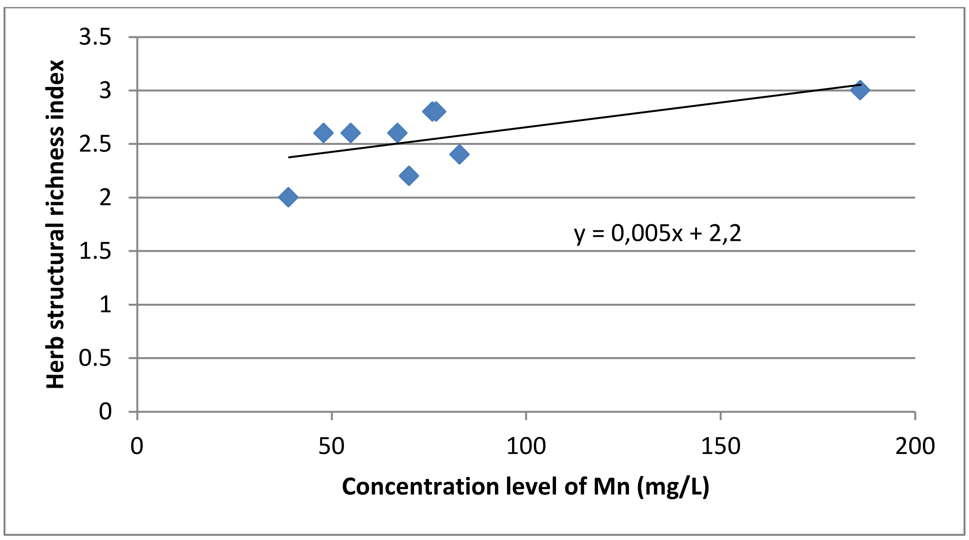

Figure 14: Herb structural richness as a function of the concentration level of Manganese (Mn) in mg/L.

Table 11: Analysis of variance for regression (Relationship between manganese concentration and herb structural richness)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.31	0.31	4.68	0.07
Residual error	7	0.47	0.07		
Total	8	0.78			

Herb structural diversity was positively related to Mn concentration (P = 0.04, r = 0.69) (Figure 15; Table 12). Therefore, herb structural richness increased as Mn concentration augmented (Figure 15). The regression equation was: Herb structural richness = 0.005 (Mn concentration) + 0.4 (Figure 15). Additionally, there was no relationship between Mn concentration and structural diversity of shrubs (P = 0.32, r = 0.38) and trees (P = 0.82, r = 0.09).

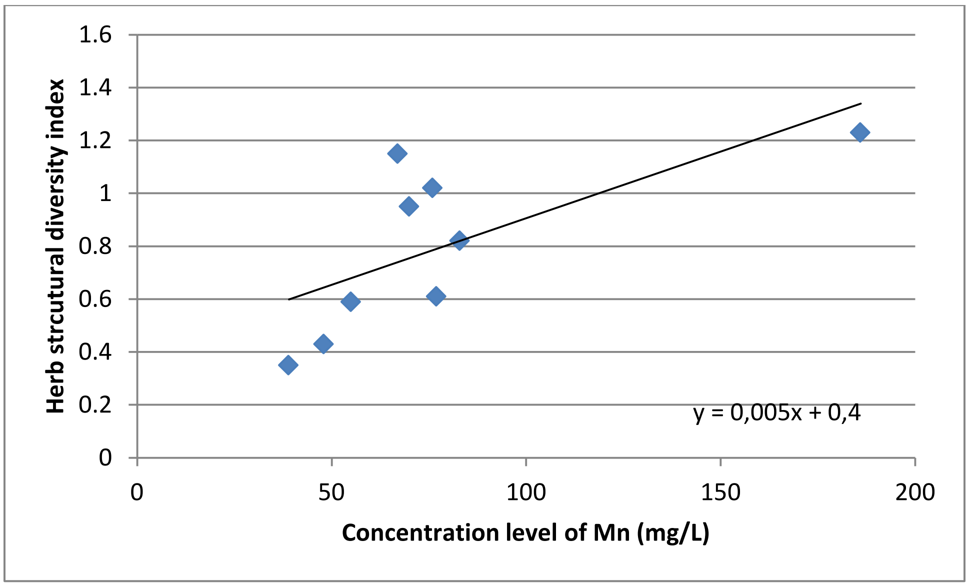

Figure 15: Herb structural diversity as a function of the concentration level of Manganese (Mn) in mg/L.

Table 12: Analysis of variance for regression (Relationship between manganese concentration and herb structural diversity)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.38	0.38	6.25	0.04
Residual error	7	0.42	0.06		
Total	8	0.80			

Relationships between Cation Exchange Capacity and the different plant biodiversity measurements

Tree species richness was inversely correlated to CEC in the soil (P-value = 0.03, r = 0.72) (Figure 16; Table 13). Accordingly, the number of tree species in a forest stand increased as CEC decreased in the soil (Figure 16). The regression equation for this relationship was: Tree species richness = -2.14 (CEC) + 41.18 (Figure 16). There was no relationship between CEC and species richness of herbs (P = 0.84, r = 0.08) and shrubs (P = 0.38, r = 0.33).

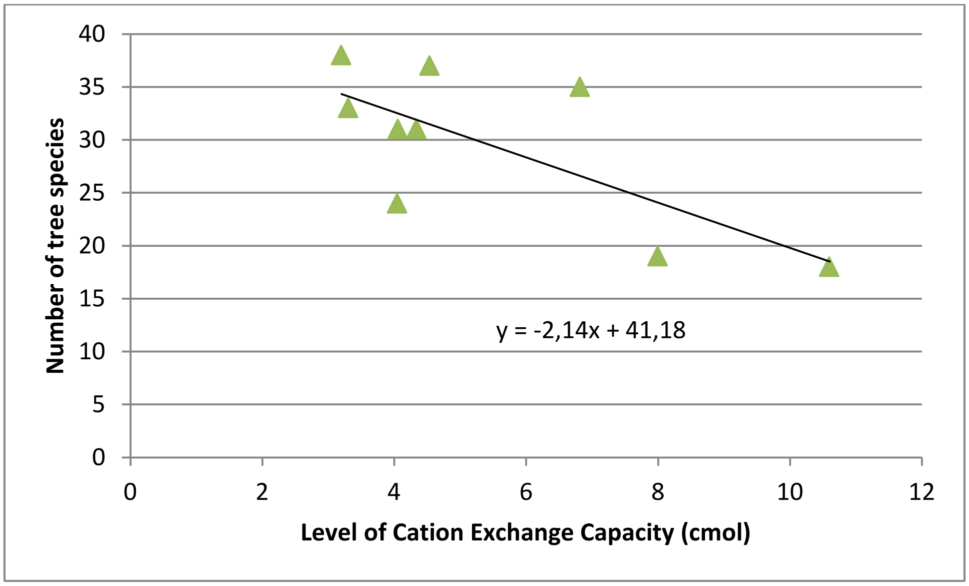

Figure 16: Tree species richness as a function of the level of Cation Exchange Capacity in cmol.

Table 13: Analysis of variance for regression (Relationship between cation exchange capacity and tree species richness)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	230.77	230.77	7.43	0.03
Residual error	7	217.45	31.06		
Total	8	448.22			

CEC was not related to Shannon-Wiener species diversity of herbs (P = 0.17, r = 0.50), shrubs (P = 0.53, r = 0.24), and trees (P = 0.79, r = 0.10), neither to Simpson's species diversity of herbs (P = 0.20, r = 0.47), shrubs (P = 0.70, r = 0.15), and trees (P = 0.72, r = 0.14). Furthermore, it was not correlated to structural richness of herbs (P = 0.24, r = 0.44), shrubs (P = 0.72, r = 0.14), and trees (P = 0.89, r = 0.06), neither to structural diversity of herbs (P = 0.48, r = 0.27), shrubs (P = 0.82, r = 0.09), and trees (P = 0.23, r = 0.45).

Relationships between C/N ratio and the different plant biodiversity measurements

There was no relationship between C/N ratio in the organic matter and species richness of herbs (P = 0.61, r = 0.20), shrubs (P = 0.83, r = 0.08), and trees (P = 0.29, r = 0.40). Also, C/N ratio was not related to Simpson's species diversity of herbs (P = 0.47, r = 0.28), shrubs (P = 0.43, r = 0.30), and trees (P = 0.11, r = 0.57), neither to structural diversity of herbs (P = 0.92, r = 0.04), shrubs (P = 0.12, r = 0.55), and trees (P = 0.85, r = 0.08).

On the other hand, tree Shannon-Wiener species diversity was found to be positively correlated to C/N ratio (Figure 17). The regression was significant (P = 0.01, r = 0.78) (Table 14). Therefore, tree species diversity (S-W) tended to increase as the C/N ratio augmented in the organic matter (Figure 17). The regression equation of this relationship was: Tree S-W species diversity = 0.02 (C/N ratio) + 2.71 (Figure 17). The other two measurements of Shannon-Wiener species diversity (Herbs with P = 0.87 and r = 0.06; Shrubs with a P = 0.39 and r = 0.33) were not related to C/N ratio.

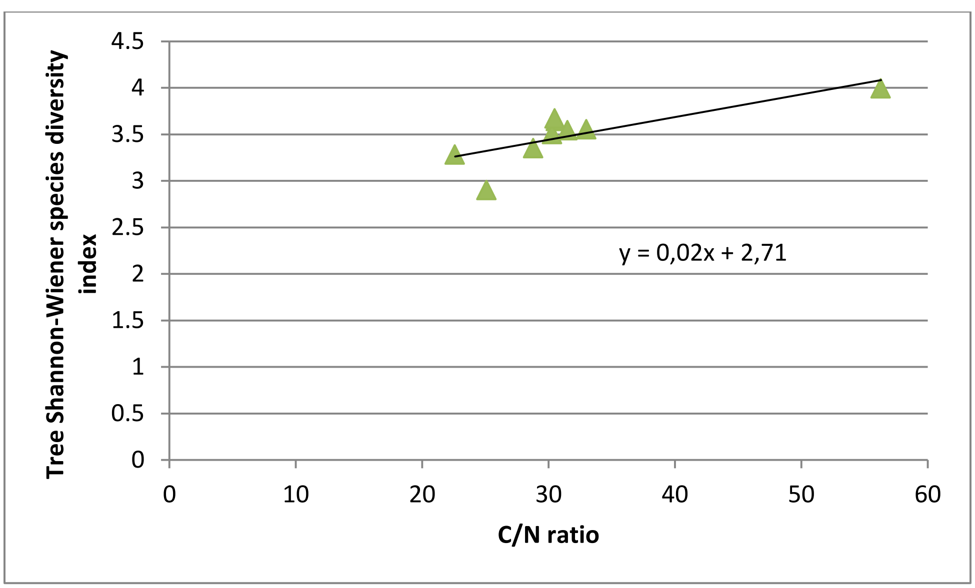

Figure 17: Tree Shannon-Wiener species diversity as a function of the level of Carbon-Nitrogen (C/N) ratio.

Table 14: Analysis of variance for regression (Relationship between C/N ratio and tree Shannon-Wiener species diversity)					
	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.44	0.44	11.12	0.01
Residual error	7	0.28	0.04		
Total	8	0.72			

Structural richness of herbs and shrubs was almost negatively correlated to C/N ratio, but the regressions were not significant (*P* = 0.09, r =0.60 and *P* = 0.10, r = 0.59 respectively) (Figure 18-19; Table 15-16). There was no relationship between tree structural richness and C/N ratio (*P* = 0.67, r = 0.17).

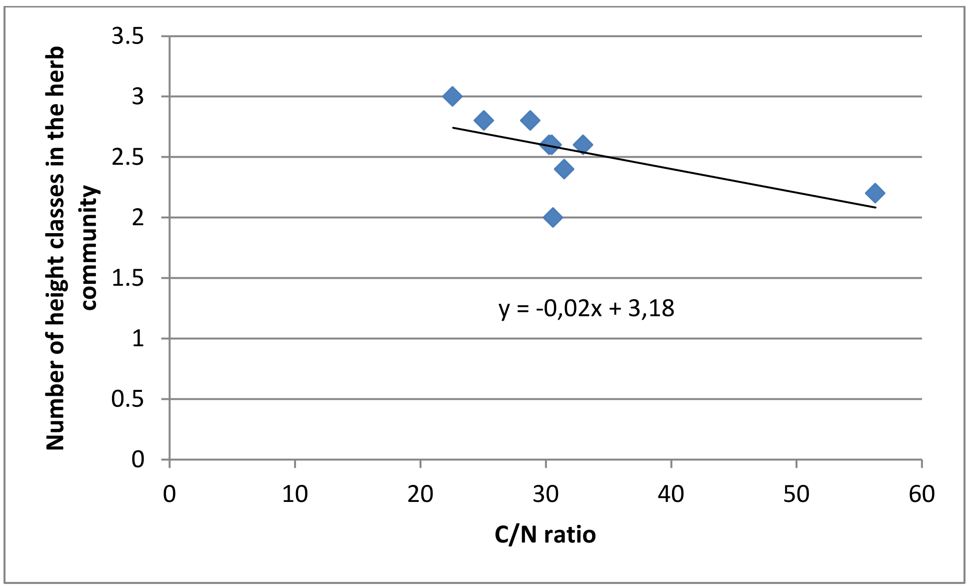

Figure 18: Herb structural richness as a function of the level of Carbon-Nitrogen (C/N) ratio.

Table 15: Analysis of variance for regression (Relationship between C/N ratio and herb structural richness)					
	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.28	0.28	3.98	0.09
Residual error	7	0.50	0.07		
Total	8	0.78			

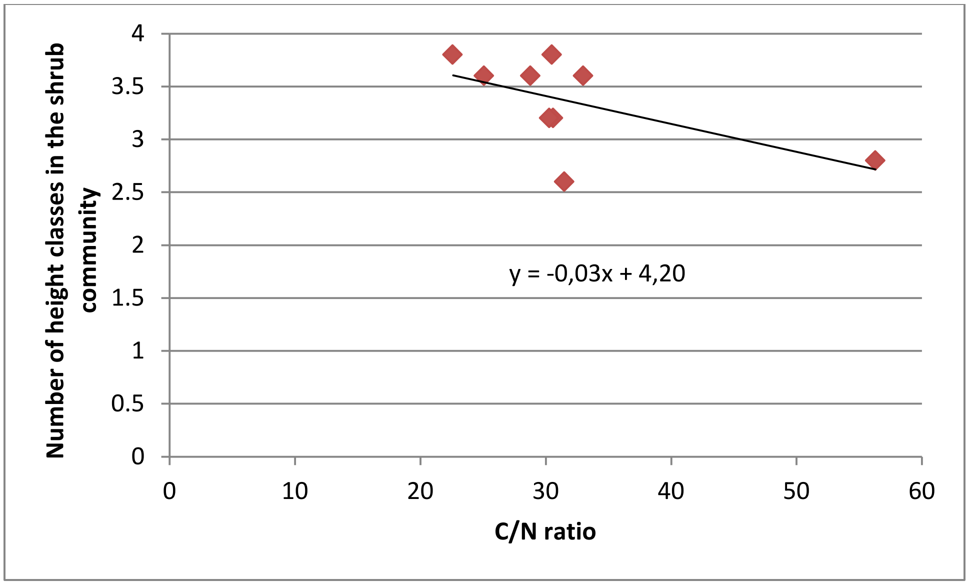

Figure 19: Shrub structural richness as a function of the level of Carbon-Nitrogen (C/N) ratio.

Table 16: Analysis of variance for regression (Relationship between C/N ratio and shrub structural richness)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.52	0.52	3.72	0.10
Residual error	7	0.98	0.14		
Total	8	1.50			

Relationships between Total Nitrogen (N) and the different plant biodiversity measurements

There was no relationship between the percentage of total N in organic matter and species richness of herbs (*P* = 0.76, r = 0.12), shrubs (*P* = 0.88, r = 0.06), and tree (*P* = 0.91, r = 0.04). In addition, the percentage of total N was not correlated to Shannon-Wiener species diversity of herbs (*P* = 0.83, r = 0.08) and shrubs (*P* = 0.44, r = 0.30). On a note, Shannon-Wiener species diversity of trees was almost inversely related to the percentage of total nitrogen (*P*-value close to 0.05), but the regression was not significant (*P* = 0.07, r = 0.63) (Figure 20; Table 17).

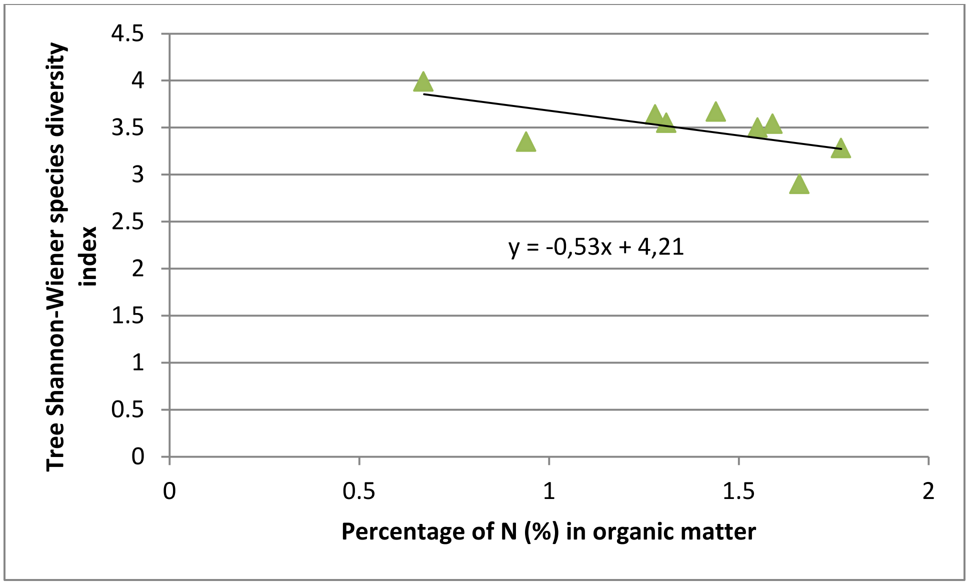

Figure 20: Tree Shannon-Wiener species diversity as a function of the percentage (%) of nitrogen in organic matter.

Table 17: Analysis of variance for regression (Relationship between nitrogen in organic matter and tree Shannon-Wiener species diversity)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.28	0.28	4.52	0.07
Residual error	7	0.44	0.06		
Total	8	0.72			

There was no relationship discovered between the percentage of total N and Simpson's species diversity of herbs (*P* = 0.98, r = 0.008), shrubs (*P* = 0.51, r = 0.25), and trees (*P* = 0.15, r = 0.52). Also, the percentage of total N was not related to structural richness of herbs (*P* = 0.20, r = 0.47), shrubs (*P* = 0.44, r = 0.30), and trees (*P* = 0.45, r = 0.29), neither to structural diversity of herbs (*P* = 0.37, r = 0.34), shrubs (*P* = 0.43, r = 0.30), and trees (*P* = 0.51, r = 0.25).

Relationships between Organic Carbon (C) and the different plant biodiversity measurements

There was no relationship between the percentage of C in organic matter and species richness of herbs (*P* = 0.79, r = 0.11), shrubs (*P* = 0.99, r = 0.005), and trees (*P* = 0.13, r = 0.55). The percentage of organic C was not correlated to Shannon-Wiener diversity of herbs (*P* = 0.58, r = 0.22), shrubs (*P* = 0.77, r = 0.11), and trees (*P* = 0.86, r = 0.07), neither to Simpson's diversity of herbs (*P* = 0.53, r = 0.24), shrubs (*P* = 0.73, r = 0.14), and trees (*P* = 0.95, r = 0.02). Additionally, the percentage of organic C was not related to structural richness of herbs (*P* = 0.69, r = 0.21), shrubs (*P* = 0.37, r = 0.34), and trees (*P* = 0.20, r = 0.47), neither to structural diversity of herbs (*P* = 0.59, r = 0.21), shrubs (*P* = 0.35, r = 0.35), and trees (*P* = 0.50, r = 0.26).

Relationships between Soil fertility index and the different plant biodiversity measurements

There was a negative relationship between tree species richness and soil fertility index (*P* = 0.01, r = 0.78) (Figure 21; Table 18). Then, we can see that the number of tree species decreased as the soil fertility index increased (Figure 21). The regression equation for this relationship was: Tree species richness = -0.37 (soil fertility index) + 41.99 (Figure 21). There was no relationship between soil fertility index and species richness of herbs (*P* = 0.88, r = 0.06) and shrubs (*P* = 0.61, r = 0.20).

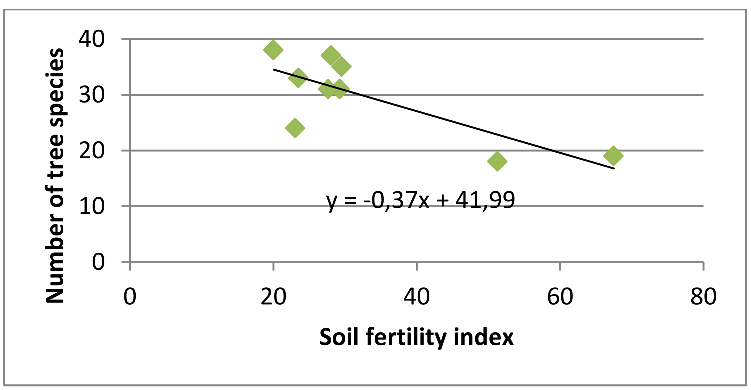

Figure 21: Tree species richness as a function of the soil fertility index.

Table 18: Analysis of variance for regression (Relationship between tree species richness and soil fertility index)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	272.99	272.99	10.91	0.01
Residual error	7	175.23	25.03		
Total	8	448.22			

Soil fertility index was not related to Shannon-Wiener species diversity of herbs (*P* = 0.15, r = 0.52), shrubs (*P* = 0.34, r = 0.36), and trees (*P* = 0.37, r = 0.34), neither to Simpson's species diversity of herbs (*P* = 0.13, r = 0.55), shrubs (*P* = 0.57, r = 0.22), and trees (*P* = 0.92, r = 0.04). Furthermore, soil fertility index was not correlated to structural diversity of herbs (*P* = 0.17, r = 0.50), shrubs (*P* = 0.29, r = 0.40), and trees (*P* = 0.42, r = 0.31), neither to structural richness of shrubs (*P* = 0.33, r = 0.37) and trees (*P* = 0.54, r = 0.24). Conversely, herb structural richness was positively related to soil fertility index (*P* = 0.04, r = 0.68) (Figure 22; Table 19). Therefore, herb structural richness increased as soil fertility index augmented (Figure 22). The regression equation for this relationship was: Number of herb height classes = 0.01 (soil fertility index) + 2.10 (Figure 22).

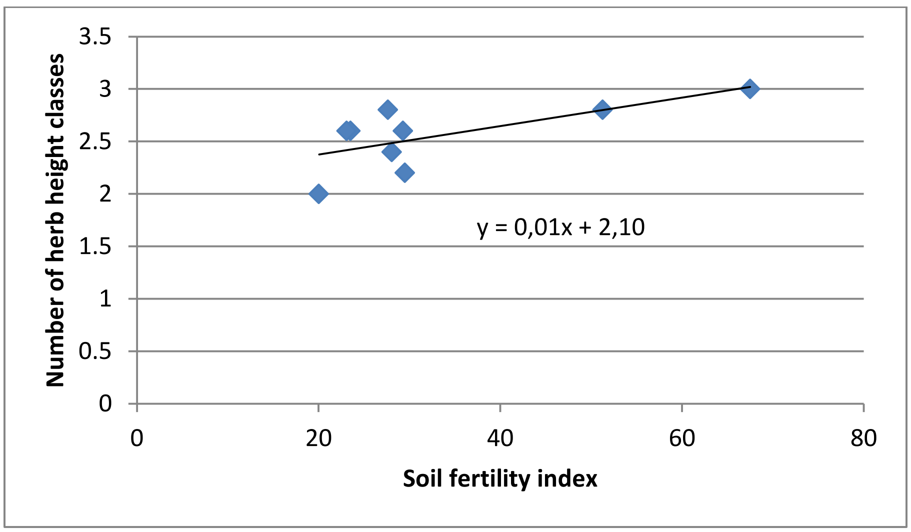

Figure 22: Herb structural richness as a function of the soil fertility index.

Table 19: Analysis of variance for regression (Relationship between herb structural richness and soil fertility index)

	Degree of freedom	*Sum of squares*	*Mean of squares*	*F*	*P-value*
Regression	1	0.36	0.36	6.06	0.04
Residual error	7	0.42	0.06		
Total	8	0.78			

Discussion

Species richness

In this study, tree species richness was found to be inversely related to concentration levels of K, Ca, and P, CEC, and soil fertility index. These results supported the hypothesis where there should be relationships between tree species richness and the different soil fertility factors: K, Ca, P, CEC, and soil fertility index. This discovery agreed with many studies that have found some kind of relationships between species richness and nutrient availability (Grime 1973; Huston 1980; Tilman 1982). Doing a study in tropical forests in Costa Rica, Huston (1980, 1993) also found a decrease in tree species richness with the increase of CEC, soil fertility index, and concentration level of K, P, and Ca. He suggested that lower fertility soil generally favoured higher tree species richness and higher fertility soil usually promoted lower tree species richness (Huston 1980, 1993). In lower fertility soil, a naturally strong tree species competitor may lack resources (nutrients) in order to outcompete the other tree species; thereby causing higher tree species richness. Furthermore, many researchers that studied the relationship between fertilization and species richness uncovered that fertilization (higher soil fertility) decreased species richness (Tilman 1982; Tilman 1983; Mittelbach *et al.* 2001). The results of these studies agree with our findings.

Many others studies done in temperate forests and agroecosystems encountered a positive relationship between tree species richness and soil factors such as soil fertility index, Ca, P, and K (Peet and Christensen 1988; Grubb 1987; Goodland 1971; Janssens *et al.* 1998; Pausas and Austin 2001). This pattern is completely different than the results obtained in our study, but we are talking about completely different ecosystems in different regions of the world. Therefore, the relationship of tree species richness to soil fertility index and concentration of K, Ca and P appears differently in tropical forests compared to temperate ecosystems. Tree species richness tends to be inversely correlated to these soil fertility factors in tropical forests and positively related in temperate ecosystems.

In this study, tree species richness was not correlated to the concentration of Mg, Fe, Cu, Zn, and Mn, the C/N ratio, nor the percentage of total N and organic C. These results do not agree with the findings of Kumar *et al.* (2010) where the percentage of total N and organic C was highly positively related to tree species richness. This difference may be generated by precipitation difference between the two ecosystems studied. Soil nutrient availability is affected by precipitation due to its influence on erosion and nutrient cycling (Huston 1980). Also, species richness tends to be affected by precipitation (Gentry 1988). Our study was accomplished in a humid tropical forest with high annual precipitation while the study of Kumar *et al.* (2010) was achieved in a dry deciduous forest with low annual precipitation. Additionally, Kumar *et al.* (2010) did not find any relationship between C/N ratio and tree species richness, and Fu *et al.* (2004) encountered no relationship between total N (%) and species richness. These two studies supported our findings. It seems that tree species richness was more affected by soil fertility than C/N ratio in our study.

Species richness of herbs and shrubs was not related to any of the soil variables. Some studies disagree with these results. Grubb (1987) and Goodland (1971) discovered a negative relationship between herb species richness and soil fertility. Wright (1992) found a positive relationship between herb and shrub species richness and soil fertility. Overall, there have not been many studies examining the relationship between soil chemical factors and species richness of herbs and shrubs. The results in the different studies about this relationship are highly variable and it may depend on the actual species themselves that are found in the different ecosystems. Moore and Keddy (1989) suggested that different patterns of species richness may be found with different species types.

Shannon-Wiener and Simpson's species diversity

In this study, Shannon-Wiener tree species diversity was only correlated to C/N ratio and it was a positive relationship. This is the first study, which I am aware, that has looked at the relationship between these two variables. Higher tree species diversity with higher C/N ratio mean that there is less N stored in organic matter compared to C in higher species diversity stands. Higher plant diversity tended to occur on poor soils (Huston 1993); therefore it is normal that there is less nitrogen that is stored in the organic matter compared to carbon in ecosystems with higher species diversity due to lack of nutrients available to the trees.

Shannon-Wiener tree species diversity was not related to any of the other soil variables (K, Ca, Mg, P, Fe, Cu, Zn, Mn, CEC, total N, organic C, and soil fertility index). There was no relationship between Shannon-Wiener diversity of herbs and shrubs and any of the soil variables. Also, Simpson's species diversity of herbs, shrubs, and trees was not correlated to any of the soil variables. These findings disagree with many studies done in temperate forests or agroecosystems. Loreau *et al.* (2007) suggested that species diversity is usually related to soil fertility. As well, Grime (1973) and Tilman and Pacala (1993) demonstrated that soil fertility has an impact on species diversity. Tilman *et al.* (1996) established that higher species diversity ecosystems have a greater capacity to utilize nutrients; thereby reducing soil nitrogen leaching loss, which tends to increase soil fertility. Janssens *et al.* (1998) found that species diversity was positively correlated to K content and declined with the increase of P content in the soil. Finally, Dybzinski *et al.* (2008) encountered that soil fertility and total N increased with species diversity. These studies may have obtained different results than us due to the different ecosystems (ecosystems of temperate regions) in which they were conducted compared to a humid tropical forest. There seems to be different trends in the relationship of plant biodiversity with soil chemical fertility between tropical and temperate ecosystems. Many ecological processes act differently in tropical compared to temperate ecosystems. A good example is soil limiting factor – N is the soil limiting factor in temperate ecosystems while P is the soil limiting factor in tropical ecosystems (Tilman *et al.* 1996; Huston 1980). Also, competition, which influences species diversity, tends to play a more important role in temperate forests compared to tropical forests due to niche partitioning by plants that occur in the tropics (Burger 1980).

In spite of these results, few researchers have obtained results similar to us. Fu *et al.* (2004) found no relationship between Shannon-Wiener diversity and the three soil factors: total N, P and K. Janssens *et al.* (1998) reported no relationship between species diversity and the two soil factors: Ca and total N. Our research is the first study that I am aware that has investigated the relationship between Simpson's and Shannon-Wiener species diversity and soil chemical factors in tropical forests.

Structural richness and diversity

The concepts of structural richness and diversity have been widely used in the domain of forestry and have become very important in silviculture management in today's world (O'Hara 1998). Forest managers often focus on increasing structural richness and diversity using management practices such as shelterwood, group or individual tree selection, and thinning in order to amplify biodiversity over the landscape (Sullivan *et al.* 2001; Montes *et al.* 2004; Krcmar *et al.* 2005; Solomon and Gove 1999; Frankin *et al.* 2002; O'Hara 1998; Pretzsch 1998). However, no research has been done with regard to the correlation between soil chemical fertility and structural richness and diversity. As far as I know, this study is the first that has looked at the relationship between these two variables.

In this investigation, herb structural richness increased significantly with the increase of soil fertility index and P concentration in the soil. Structural richness was not related to any other soil factors. P is considered the main soil factor that limits growth of plants in tropical ecosystems (Holl

1999) and is the most important soil factor determining soil fertility (Huston 1980). Therefore, the herb community may be able to grow taller in soil with higher P content and soil fertility leading to higher herb structural richness. Also, herb structural diversity was positively related to Mn concentration in this research. Structural diversity was not correlated to any other soil factors. Our findings agree with the results obtained by Lindgren and Sullivan (2001) where fertilization (higher soil fertility) did not change structural diversity of herbs, shrubs, and trees. Mn tended to not affect soil fertility compared to other soil elements such as P, K, Ca, and N. We found that the other measured soil factors were not related to structural diversity. Therefore, structural diversity seemed to be not affected much by soil fertility.

Factors that might have affected the results

Many studies found other factors that were related to plant biodiversity or soil chemical fertility. Mycorrhizal fungi can enhance nutrient availability in soil (Wardle *et al.* 2004). Different mycorrhizal fungus communities can influence differently soil fertility (Klirinomos *et al.* 2000). Plant diversity and N availability significantly increase with the increase in fungal community (Zak *et al.* 2003). Soil animals can augment decomposition rate; thereby increasing the availability of plant nutrients such as P, Mn, Fe, Zn, and Cu in the soil (Altieri 1999). Soil nutrient concentration is affected by precipitation which influences nutrient cycling, leaching, and erosion (Huston 1980). Brady and Weil (1999) suggested that soil water content is the most powerful control on the rate of soil chemical and biological activities. Pausas *et al.* (2001) found a tendency in which species richness increased when there was more water available in the soil. Fu *et al.* (2004) demonstrated that elevation and topography highly influenced species richness and diversity. Small disturbances such as natural tree falling caused by windthrow or insect and disease infection, which are very common in tropical forests, tended to alter structural richness and diversity (Sullivan *et al.* 2000; Swanson *et al.* 2011; Lindgren and Sullivan 2001). All factors previously mentioned may have affected the results obtained during the investigation because this study was accomplished in a mature primary forest in which it was not possible to control them.

Future studies

Future studies on this subject should focus on long-term research in which the effect of plant biodiversity on soil chemical fertility could be tested by controlling plant biodiversity and other environmental factors. Also, the effect of soil chemical fertility on plant biodiversity could be evaluated by controlling the different soil factors and other environmental factors. This kind of long-term research has never been done in tropical ecosystems. Furthermore, it would be interesting to investigate the relationship of plant biodiversity with all the possible natural factors and processes that can affect it in the different ecosystems of tropical and temperate regions. Multiple linear regressions of the different possible relationships could be analyzed and we could understand better the correlation between all of them.

Acknowledgement

I would like to express my gratitude to all the people who gave me the possibility to complete this thesis. I want to thank Director Ronald Sanchez for giving me the opportunity to collect all my data in the ‘’Reserva Biológica Alberto Manuel Brenes’’ in Costa Rica and the administration of the company ‘’Cafesa’’ for analyzing my soil samples so close to the Christmas holiday. Furthermore, I have to thank my two assistants, Melissa Diaz Morales and Felipe Vega, for taking the time to come with me in the field to collect all the data for this thesis and Professor Carlos Morales of the University of Costa Rica for taking the time to help me identify plant species that I was not able to do in the field. Finally, I want to give special thanks to Professor Dr. Tom Sullivan of the University of British

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Appendix: Field data

Table 20: Herb biodiversity measurements in each of the nine sampling plots						
Sampling plot	Total volume (m^3/0.01ha)	Species richness (# of species)	Shannon-Wiener species diversity	Simpson's species diversity	Structural richness	Structural diversity
1	64.6	10	2.15	0.71	2	0.35
2	26	11	2.34	0.7	2.4	0.82
3	163.5	7	1.94	0.71	2.6	1.15
4	102.84	11	1.79	0.65	2.6	0.43
5	132.98	10	2.47	0.74	2.6	0.59
6	43.73	8	1.76	0.55	2.8	1.02
7	76.45	9	2.36	0.77	2.8	0.61
8	44.075	10	2.5	0.78	3	1.23
9	32.9	10	2.1	0.63	2.2	0.95

Table 21: Shrub biodiversity measurements in each of the nine sampling plots						
Sampling plot	Total volume (m^3/0.01ha)	Species richness (# of species)	Shannon-Wiener species diversity	Simpson's species diversity	Structural richness	Structural diversity
1	168.74	17	2.8	0.81	3.2	1.5
2	210.08	13	2.16	0.63	2.6	0.64
3	172.12	14	2.38	0.76	3.2	0.69
4	840.73	24	3.09	0.82	3.8	1.26
5	332.59	18	1.79	0.53	3.6	1.32
6	446.26	17	2.55	0.75	3.6	1.34
7	1568.03	15	2.33	0.69	3.6	1.2
8	1109.42	17	2.1	0.67	3.8	1.76
9	299.7	16	2.83	0.82	2.8	0.74

Table 22: Tree biodiversity measurements of each of the nine sampling plots						
Sampling plot	Total volume (m^3/0.01ha)	Species richness (# of species)	Shannon-Wiener species diversity	Simpson's species diversity	Structural richness	Structural diversity
1	10611.08	38	3.64	0.87	3.4	0.83
2	12752.5	37	3.54	0.88	3.6	0.57
3	14869.28	31	3.5	0.88	4	0.58
4	19460.2	33	3.67	0.91	3.2	0.29
5	16728.19	24	3.55	0.89	3.4	0.45
6	15000.33	31	2.9	0.78	3.4	0.73
7	17721.15	18	3.35	0.88	3	0.32
8	16241.25	19	3.28	0.87	4	0.51
9	22638.045	35	3.99	0.92	3.8	0.52

Table 23: Data of soil analysis (pH, K, Ca, Mg, Extractable acids) for each of the nine sampling plots

Sampling plot	pH (H_2O)	K (cmol(+)/L)	Ca (cmol(+)/L)	Mg (cmol(+)/L)	Extractable acids (Al+H) (cmol(+)/L)
1	4.6	0.19	1.73	0.22	1.06
2	4.6	0.21	2.76	0.54	1.03
3	4.8	0.21	2.55	0.55	1.03
4	4.8	0.17	1.92	0.22	1
5	4.7	0.11	2.65	0.54	0.75
6	4.5	0.19	2.33	0.44	1.1
7	4.6	0.39	6.78	1.83	1.6
8	5.2	0.53	5.12	1.25	1.1
9	5.2	0.16	5.09	1.32	0.25

Table 24: Data of soil analysis (P, Fe, Cu, Zn, Mn) for each of the nine sampling plots

Sampling plot	P (mg/L)	Fe (mg/L)	Cu (mg/L)	Zn (mg/L)	Mn (mg/L)
1	3	67	4	1.1	39
2	5	61	5	3	83
3	6	98	4	3.7	67
4	5	67	5	2.2	48
5	5	47	4	1.9	55
6	6	66	5	1.9	76
7	6	64	4	1.9	77
8	14	142	5	2.3	186
9	3	60	6	1.9	70

Table 25: Data of soil analysis (SDA, SDC, CEC, Ca/Mg, Ca/K) for each of the nine sampling plots

Sampling plot	Saturated acids (SDA) (%)	Sum of cations (SDC) (cmol)	Cation exchange capacity (CEC) (cmol)	Ca/Mg ratio	Ca/K ratio
1	33.13	2.14	3.2	7.86	9.11
2	22.69	3.51	4.54	5.11	13.14
3	23.73	3.31	4.34	4.64	12.14
4	30.21	2.31	3.31	8.73	11.29
5	18.52	3.3	4.05	4.91	24.09
6	27.09	2.96	4.06	5.3	12.26
7	15.09	9	10.6	3.7	17.38
8	13.75	6.9	8	4.1	9.66
9	3.67	6.57	6.82	3.86	31.81

Table 26: Data of analysis of soil and organic matter (Mg/K, (Ca+Mg)/K, C/N ratio, total N, organic C)

Sampling plot	Mg/K ratio	(Ca+Mg)/k ratio	C/N ratio	Total N (%)	Organic C (%)
1	1.16	10.26	30.6	1.28	39.2
2	2.57	15.71	31.5	1.59	50.1
3	2.62	14.76	30.3	1.55	46.9
4	1.29	12.59	30.5	1.44	43.8
5	4.91	29	33	1.31	43.1
6	2.32	14.58	25.1	1.66	41.5
7	4.69	22.08	28.8	0.94	26.9
8	2.36	12.02	22.6	1.77	40
9	8.25	40.06	56.3	0.67	37.7